

An Extinct Lizard of the Genus *Leiocephalus* from Jamaica

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THE iguanid lizard genus *Leiocephalus* is now confined to the West Indies where it occurs on almost all islands except Jamaica and those islands to the south and east of Hispaniola. An extinct species has been described from the Late Pleistocene of Barbuda, and another form apparently became extinct on Martinique in this century (Etheridge, 1964a). The former existence of these two species led me to suggest that *Leiocephalus* might have occurred throughout the Lesser Antillies and on Puerto Rico in the not-too-remote past. An extinct species is also known from the Late Pleistocene of Hispaniola (Etheridge, 1965) and from the Early Miocene of Florida (Estes, 1963).

The discovery of an extinct species of *Leiocephalus* in several Jamaican cave deposits indicates that the range of the genus during the Late Pleistocene may actually have included virtually all islands of the West Indies.

JAMAICAN LOCALITIES

Dairy Cave. The best known fossil deposits in Jamaica are found in Dairy Cave (Fig. 1), about 2.5 km west of Dry Harbour (now known as Discovery Bay) in St. Anns Parish; 18°27'25" N, 77°22'38" W. Koopman and Williams (1951) and Hecht (1951) have given general descriptions of the cave. Some fossils of *Leiocephalus* were collected here by Dr. Harold E. Anthony in 1919 and 1920. The probable site of Anthony's collection has been determined by Dr. Walter Auffenberg at about 200 feet west southwest of the main entrance. It is designated in Auffenberg's field notes for 1958 and on the map (Fig. 1) as Locality E.

In 1958 Dr. Auffenberg obtained additional fossils of *Leiocephalus* from two other localities within Dairy Cave. One of these, designated Locality G, is about 25 feet south southwest of Anthony's site. The bones were recovered from a small amount of matrix taken from two solution holes in the wall, about 12 feet above the cave floor. The second site, Locality D, was discovered in a roughly circular chamber about 15 feet across and 10 feet high, near the eastern end of the cave. According to Auffenberg's field notes much of the matrix has been removed in phosphate mining. The original floor of flow stone is about three feet below the

limestone floor, and is provided with pillars of travertine connecting the old floor with the ceiling. Below this is a series of beds, more or less consolidated near the top, more clayey near the bottom. About four feet above the original floor is a layer of shell. Below this the shell layer gradually gives way to layers of dark reddish clay. The fossils of *Leiocephalus*, together with those of other lizards and mammals, from this locality are from the lower layers of clay. In his field notes Auffenberg suggests the likelihood that this layer was contemporaneous with Anthony's "lizard layer".

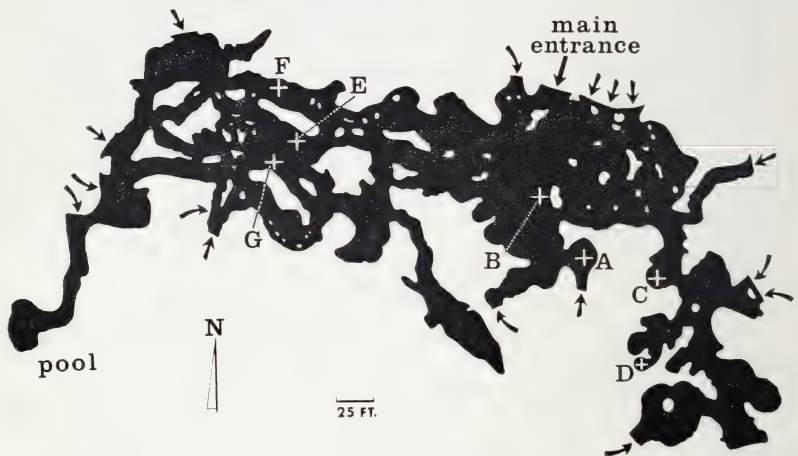


Fig. 1. Map of Dairy Cave, St. Anns Parish, Jamaica. Prepared from a map originally drawn and surveyed by the Jamaica Geological Survey. Entrances to the cave are indicated by arrows. Localities from which fossils have been obtained are indicated by crosses and are designated A through G.

Montego Bay Airport Cave. This site was discovered by Auffenberg on June 28, 1957, near the west end of the air strip at Montego Bay, St. James Parish; $18^{\circ}30'22''$ N, $77^{\circ}54'11''$ W. According to his field notes the cave is fairly large but much of it has been dug out in mining for phosphate. In one of the large chambers at the eastern edge of the main entrance to the cave he located a bone-bearing deposit below the former travertine floor. The cave earth there is semiconsolidated, reddish in color and contained an abundance of broken shells and bone. The bone is yellowish in color and chalky in consistency. The very dark red color of the beds led him to believe that these deposits are very

old, with no possibility of recent mixture as seems to be the case for some fossil lizards in Dairy Cave (Auffenberg, field notes, 1957). The fossil lizards were collected by Auffenberg during this visit, and again in June 1958.

Portland Ridge Caves. Several fossiliferous caves have been explored in Portland Ridge, Clarendon Parish. One of these, designated Portland Cave I by Auffenberg, was discovered by Dr. H. E. Anthony in 1919 or 1920, and has been described by Koopman and Williams (1951). The fossil *Leiocephalus* from this cave were obtained by Dr. Auffenberg on July 7, 1957. According to his field notes of that year the fossils were taken at Locality E, near the end of the left, i.e., south, passage. Three beds may be distinguished at this locality: Bed 3, about 2 feet deep from the surface, is composed of fine soil, grayish at the surface and grading to reddish at its base; Bed 2 lies below this, 3 to 8 inches deep, comprised of pebbly, red, slightly consolidated earth, containing many bones, most of which are of white color; and Bed 1, about 8 inches deep, whitish and extending to the limestone, containing bones that are blackish. The bones of *Leiocephalus* were taken from Bed 2.

A second cave in Portland Ridge, designated Portland Cave III, is located about 1000 feet southwest of Portland Cave I. Fossil *Leiocephalus* were collected here by Dr. Ernest E. Williams in 1953. According to Auffenberg's field notes of 1957 the cave is small and provided with two openings, one at the north end and one at the south end. To the east it is connected with a very large and deep cave on a lower level. In a test pit Auffenberg located a bone-bearing layer about 4 feet down from the surface, just above a layer of white earth. The *Leiocephalus* bones collected by Williams near the south entrance may have come from this layer.

Leiocephalus jamaicensis new species

Holotype. A left dentary, No. 2311 in the vertebrate paleontology collections of the American Museum of Natural History. Collected by H. E. Anthony in 1919 or 1920.

Type Locality. Dairy Cave, about 200 feet west southwest of the main entrance (Locality E), 2.5 km west of Dry Harbour, St. Anns Parish, Jamaica; 18°27'25" North Latitude, 77°22'38" West Longitude. Probably Late Pleistocene.

Referred Specimens. (AMNH = American Museum of Natural History; UF = University of Florida, the Florida State Museum). Dairy Cave, Loc. E: maxillae AMNH 2312-3, parietal AMNH 2314, caudal vertebrae AMNH 2315. Dairy Cave, Loc. D: dentaries UF 8503-4. Dairy Cave, Loc. G: dentary UF 8502. Montego Bay Airport Cave: dentary UF 8505, parietal UF 8506, frontal UF 8508, pterygoid UF 8509, caudal vertebrae UF 8510. Portland Cave I, Loc. E: dentaries UF 8511-2, maxilla UF 8513, pterygoid UF 8514, body vertebrae UF 8516 (2), caudal vertebrae UF 8518 (3). Portland Cave III: dentaries UF 8489-90, maxillae UF 8491-3, articular-surangular UF 8494, premaxillae 8495 (2), frontal UF 8496, caudal vertebrae UF 8497 (5), 8500, body vertebrae UF 8501 (2).

Diagnosis. A large species of *Leiocephalus* apparently allied to *L. melanochloris*, *L. schreibersi* and *L. inaguae*, from which it differs only in having attained a greater maximum size. Its maximum snout-vent length was at least 130 mm, as great as the largest living form, *L. carinatus microcyon*, and may have been as large as 170 mm. The maximum recorded snout-vent lengths of *melanochloris*, *schreibersi* and *inaguae* are 108 mm, 90 mm and 73 mm respectively.

Leiocephalus jamaicensis also differs from *L. carinatus*, *L. punctatus*, and *L. loxogrammus* in lacking pterygoid teeth, from *L. personatus* and *L. pratensis* in that the surface rugosities of the frontal and parietal bones do not form a pattern of the overlying scales, from *L. apertosulcus* in having a closed Meckelian canal, from *psammodomus*, *greenwayi*, *cubensis*, *punctatus* and *stictogaster* in that the anterior border of the angular process of the articular bones forms an obtuse angle rather than a right or acute angle with the medial border of the articular, from *macropus*, *loxogrammus*, *personatus* and *raviceps* in that the main axis of the articular process projects medially rather than posteromedially from the articular condyle, and from *cuneus* in that the articular and retroarticular processes are not separated by a distinct indentation.

Description of Type. The nearly complete left dentary is 16.5 mm long from its broken posterior border to the symphysis. Its tooth row, measured in a straight line from the projected anterior border of the first tooth to the projected posterior border of the last tooth (both are missing) is 12.8 mm long. The height of the

dentary at the position of the next-to-last tooth is 3.1 mm. There are 24 teeth or vacant alveoli; missing are (front to back) teeth number 1, 6, 8, 10, 17, 22 and 24. The second and third teeth are bluntly conical and curve inward and slightly backward. The fourth and fifth teeth are similar to these except that there is a slight posterior cusp near the base of the crown in each. The crown of the seventh tooth is very slightly flared, compressed linguo-labially, and has a small anterior and posterior cusp below the median one. The eleventh tooth and all of the more posterior ones have a crown that is flared in an anterior-posterior direction, linguo-labially compressed to form a moderately sharp cutting edge, strongly tricuspid and curved inward. The anterior and posterior cusps of each tooth are smaller than the median cusp and separated from it by a wide groove that fades out at the base of the crown. The occlusal edge of each of these teeth is slightly oblique to the main axis of the tooth row. All of the tricuspid teeth are crowded closely together so that the anterior cusp of each tooth is overlapped labially by the posterior cusp of the preceding tooth. Below their flared crowns the shaft of each tooth expands gradually toward its ankylosed base. About 40 percent of each tooth rises above the alveolar border of the dentary. A vertical row of very small foramina is visible in the lingual face of the dentary in the narrow spaces between the teeth.

The labial and ventral faces of the dentary are smooth, except where the most superficial layers of bone have been eroded away or scraped in preparation. The lower half of the labial face and the ventral face are convex. The upper half of the labial face is convex anteriorly, becoming flattened to slightly concave and lightly scored posteriorly. A large, shallow, triangular and slightly concave depression in the upper half of the posterior labial face of the dentary extends forward to the level of the twentyfirst tooth, marking the former position of the anterolateral process of the coronoid. Four mental foramina form a row in the labial face between the second and thirteenth tooth.

A large, > shaped indentation in the posterior border of the lingual face of the dentary extends forward to the level of the posterior border of the twentyfirst tooth, marking the former position of the angular and splenial. Anterior to the apex of this indentation (the former anterior border of the anterior inferior alveolar foramen) the lingual face is shallowly concave to the

level of the nineteenth tooth, and smoothly convex beyond this point. Meckel's canal penetrates the anterior end of the dentary as a small opening just below and behind the symphysial surface.

Additional Dentaries. Three additional dentaries from Dary Cave, two from Portland Cave I, two from Portland Cave III, and one from Montego Bay Cave are referred to this species. Two complete dentaries measure 12.8 mm and 12.4 mm along their tooth rows and contain 24 and 21 teeth and vacant alveoli respectively. The first 11 teeth are missing in one of these specimens and the remaining teeth have flared, strongly tricuspid crowns as in the type. In the other the crowns of the first seven teeth are simply pointed, the eighth tooth is tapered and weakly tricuspid, the ninth tooth is missing and the tenth and all of the more posterior teeth have flared and strongly tricuspid crowns. In a partial dentary the crowns of the first five teeth are simply pointed, the sixth is missing, the seventh is tapered and weakly tricuspid, the eighth and ninth are missing and the tenth and all of the more posterior teeth are flared and strongly tricuspid. Thus, the transition from simply pointed anterior teeth to flared and strongly tricuspid posterior teeth may begin as far forward as the fourth tooth and be completed as far posteriorly as the ninth.

Maxillae. Two maxillae from the type locality, 3 from Portland Cave III and one from Portland Cave I are referred to this species. Two complete specimens measure 8.8 mm and 11.9 mm along their tooth rows and contain 18 and 20 teeth plus vacant alveoli respectively. In the smaller specimen the first two teeth are simply pointed, the third is missing, the fourth is tapered and weakly tricuspid and the fifth and all of the more posterior teeth are flared and strongly tricuspid. In the larger specimen the first three teeth are simply pointed, the fourth is tapered and weakly tricuspid, the fifth and sixth are missing and the seventh and all more posterior tooth crowns are flared and strongly tricuspid.

Premaxillae. Two premaxillae from Portland Cave III contain seven teeth or vacant alveoli; one median tooth flanked by three on each side. The crowns of all of the teeth are simply pointed and curved slightly backward. They measure 4.0 and 4.5 mm across the widest part of the rostrum. The former positions of the overlapping nasal bones are indicated by smooth sutural scars on the dorsal surface of the slender nasal process.

Frontals. One frontal from Portland Cave III and another

from the Montego Bay Airport Cave may be definitely assigned to the genus *Leiocephalus* because of their sharply projecting crista cranii, a feature which distinguishes this genus from *Anolis*, the only other iguanid genus in the caves. However, the two frontals differ in their shape and ornamentation and possibly do not come from the same species. If they do not, then it is uncertain which one of them should be assigned to *L. jamaicensis*.

The Portland Cave specimen is 3.8 mm wide across its narrowest interorbital distance and is estimated to have been about 8.6 mm wide across its parietal border. Heavy rugosities ornament the entire dorsal surface and orbital margins of the bone but do not form a regular pattern corresponding to the scales which overlayed them. A deep, narrow, oval notch in the parietal border indicates the former position of the parietal foramen.

The Montego Bay specimen is 2.5 mm wide across its narrowest interorbital width and is estimated to have been about 9.6 mm wide across its parietal border. Thus, the orbital borders are more strongly concave than in the Portland Cave specimen. In addition, the dorsal surface of the element is smooth, and a wide, shallow indentation in the parietal border indicates the former position of the parietal foramen.

Parietals. A nearly complete parietal, broken in preparation, from the type locality and a fragment of another from the Montego Bay Airport Cave are referred to this species. The Dairy Cave specimen is 10.6 mm wide across its frontal border. The lateral borders of the roof converge strongly toward the occipital border, which has been broken away. Strong rugosities, similar to those of the frontal from Portland Cave, ornament the dorsal surface of the roof. The Montego Bay specimen, though fragmentary, is obviously from a smaller individual. The lateral roof borders converge posteriorly but remain widely separated at the occipital border. Its upper surface, though not completely smooth, is much less rugose than that of the Dairy Cave specimen.

Pterygoids. A nearly complete pterygoid from Portland Cave and part of another from Montego Bay Airport Cave are referred to this species. The anterior end of the palatine process and the posterior end of the pterygoid process are broken away in the Portland Cave specimen. It is 5.2 mm wide between the postero-medial corner of the palatine plate and the lateral extremity of the ectopterygoid process, and 1.5 mm wide across the narrowest

part where the palatine plate meets the pterygoid process. The ventral surface of the palatine plate is perfectly smooth, without the slightest trace of teeth or alveoli.

The Montego Bay specimen lacks the distal parts of the palatine, pterygoid and ectopterygoid processes. It is 1.9 mm wide across the narrowest part where the palatine plate meets the pterygoid process. The ventral surface of its palatine plate is also smooth and lacks all evidence of teeth or alveoli.

Articular + Surangular. A fused articular + surangular from Portland Cave III is 16.6 mm long from the posterior end of the retroarticular process to the broken anterior end of the surangular; about one mm should be added to this for the length of the intact element.

The short, robust angular process projects medially from the articular condyle for a distance of 2.4 mm. Its upper surface is smoothly convex. Distally the process curves slightly upward. The anterior border of the process curves irregularly forward toward the medial border of the articular. The retroarticular process projects posteriorly from the condyle for a distance of 2.6 mm and is 2.6 mm wide at the condyle. Its medial, lateral and posterior borders are somewhat raised, surrounding a shallow, more or less rectangular depression. The retroarticular and angular processes are united posteromedially by a thin shelf whose margin forms a very shallow sigmoid curve between the distal extremities of the two processes.

Caudal Vertebrae. Five posterior segments of autotomic caudal vertebrae from the type locality, four posterior segments, one anterior segment, an intact autotomic vertebra and nine vertebrae from the anterior, nonautotomic part of the tail from Portland Cave III, and one posterior segment from the Montego Bay Airport Cave are referred to this species.

The centrum of the largest nonautotomic vertebra is 5.0 mm long, including its condyle. Well developed zygosphenes are present on a median projection of the neural arch between the prezygapophyses, and corresponding zygantra are present between the postzygapophyses. The neural spine is strongly compressed and tapered. A thin, median crest rises above the neural arch, sloping steeply downward from the neural spine to the interzygapophyseal projection of the arch. The centrum is strongly compressed ventrally to form a blunt, median keel below. The trans-

verse processes are wide and flat, slightly tapered toward their distal extremities, and oriented posterolaterally.

Measurements of the intact autotomic vertebrae are: greatest length of the centrum, including its condyle 6.0 mm, length of the anterior segment from the anterior ventral border of the centrum to the fracture plane 1.0 mm, length of the posterior segment from the fracture plane to the anterior ventral border of the condyle 3.2 mm, width of the centrum posterior to the plane of fracture 1.2 mm. Moderately well developed zygosphenes and zygantra are present on a small median projection of the neural arch between the prezygapophyses and corresponding zygantra are present between the postzygapophyses. A thin, median crest rises vertically above the neural arch between the neural spine and the fracture plane. It ascends abruptly above the plane as a thin, spine-like projection, then abruptly descends to the neural arch of the anterior segment. The fracture plane passes more or less vertically through the spine, down through the neural arch, curves posteriorly around the bases of the transverse processes and continues vertically down through the centrum. The dissociated segments of the other autotomic caudal vertebrae are similarly constructed; however their proportions differ greatly, due, no doubt, to their different points of origin from the caudal vertebral column.

Body Vertebrae. Two body vertebrae from Portland Cave I and two from Portland Cave III are referred to this species. The largest, apparently from near the middle of the body, has a centrum, including its condyle, 5.9 mm long. Zygosphenes and zygantra are moderately well developed. The neural spine is robust, strongly compressed and wider at the top than at the base. The sharp anterior border of the spine slopes steeply downward to the neural arch, and continues forward as a low, median neural crest. The centrum is strongly compressed ventrally to form a blunt, median keel.

Maximum Size. The snout-vent lengths of the animals from which the fossils came have been calculated by multiplying various measurements of the fossils by the ratio of measurements of the same elements of skeletons of modern species to their snout-vent lengths. Assuming that the proportions which existed in the extinct species fall within the limits of those which exist among all living forms, a minimum and maximum estimate of snout-vent length may be obtained for each fossil of the extinct species. The

minimum and maximum estimates for the largest fossil of each of several elements are as follows: dentary 90-120 mm, maxilla 111-120 mm, frontal 109-134 mm, parietal 107-131 mm, and articular-surangular 130-170 mm. Thus, *L. jamaicensis* probably reached a maximum size of at least 130 mm and may have reached a maximum size as great as 170 mm.

Comparisons. The fossils described here are referred to the genus *Leiocephalus* on the basis of numerous osteological characteristics which distinguish that genus from the related South American genera *Stenocercus*, *Tropidurus*, *Ctenoblepharis*, *Lio-laemus*, *Urocentron*, *Proctotretus*, *Platynotus*, *Plica*, and *Ophryoesoides* (Estes, 1963; Etheridge, 1964a, 1965, 1966a). The osteological characteristics which distinguish these genera, the tropidurines, from other groups of iguanid lizards have been given by Etheridge (1964b).

Slight but consistent structural differences in the skeleton may be used to differentiate most of the living and extinct species of *Leiocephalus*. Those which distinguish *L. jamaicensis* are given in the diagnosis. Although these differences are useful for the identification of fossil bones, most of them are not of the sort that may be used to indicate the phylogenetic relationships of the species to one another. For this reason little can be said as to the probable relationships of *L. jamaicensis* to other forms, except that since it can be distinguished from *L. schreibersi*, *L. melanochloris*, and *L. inaguae* only by its larger maximum size, it is probably most closely allied to those forms.

The maximum snout-vent length attained by any living species is 130 mm, recorded for *L. carinatus microcyon* (Schwartz, 1959). *L. hermimeri*, which apparently became extinct on Martinique in this century, reached 139 mm (Boulenger, 1885). The extinct forms *L. cuneus* of Barbuda and *L. apertosulcus* of Hispaniola apparently reached a maximum snout-vent length of about 200 mm (Etheridge, 1964a, 1965). Only two living species have been reported as fossils: *L. personatus* from Cerro de San Francisco, Dominican Republic, (Etheridge, 1965) and *L. carinatus* from New Providence Island (Etheridge, 1966b). The maximum size of these fossils is approximately equal to that attained by modern populations of the same species at those localities today.

Other living species of West Indian lizards are known as fossils and a number of them grew to a larger size than in modern

populations from the same area; e.g. *Anolis leachii* on Barbuda, *Anolis ricordi* on Hispaniola, and *Anolis sagrei* on New Providence. In these species the ontogenetic gradients known to exist in modern populations are continued in the fossils to a greater maximum size. Hecht (1951) described an extinct Jamaican gecko, *Aristelliger titan*, which attained a maximum size greater than the largest living species. However, there appears to be no structural difference between *A. titan* and the modern Hispaniolan species *A. lar* that cannot be accounted for solely on the basis of the larger size of *A. titan* (Etheridge, 1965). Thus there are no anatomical reasons for not considering *A. titan* to have been a Jamaican population of *A. lar* that grew to a larger size than does the present population of the species on Hispaniola. *Leiocephalus jamaicensis* may be distinguished from *schreibersi*, *melanochloris*, and *inaguae* only by its greater maximum size. As is the case of *A. titan* and *A. lar*, decision to recognize *L. jamaicensis* as an extinct species, rather than as a large Jamaicana representative of *L. melanochloris*, *L. schreibersi*, or *L. inaguae*, must be made on some grounds other than anatomical comparisons.

In my description of the Barbudan form, *L. cuneus* (Etheridge, 1964a), I failed to come to grips with the problem of distinguishing it from *L. herminieri* of Martinique. *L. cuneus* differs from all living species in the extreme anterior position of the transition from simple to tricuspid teeth; however, I have no information as to the position of this transition in the now extinct *L. herminieri*. *L. cuneus* grew considerably larger than *L. herminieri*, but the possibility remains that *L. cuneus* merely represents a population of *L. herminieri* that lived on another island and grew to a larger size.

DISCUSSION

Leiocephalus, *Stenocercus*, *Tropidurus*, *Ctenoblepharis*, *Liolaemus*, *Urocentron*, *Proctotretus*, *Platynotus*, *Plica*, and *Ophryoesoides* appear to form a group of related genera, the tropidurines, within the family Iguanidae, and their closest allies appear to be the sceloporine genera of North America, *Sceloporus*, *Uta*, *Urosaurus*, *Petrosaurus*, *Sator*, *Uma*, *Callisaurus* and *Holbrookia* (Etheridge, 1964b). *Leiocephalus* is the most distinctive genus among the tropidurines; that is, the skeletal and integumentary differences between it and the other tropidurine genera are greater than

those between any other two tropidurine genera (Etheridge, 1966a). The existence of *Leiocephalus* in the Early Miocene of Florida (Estes, 1963) indicates that the peculiar specializations of the genus were attained by at least mid-Cenozoic, and therefore the divergence between the tropidurines and sceloporines must have occurred at a still earlier time.

Two possibilities are apparent. 1) Sceloporines and tropidurines may have coexisted in North and Middle America during the mid-Cenozoic, and that following the migration of *Leiocephalus* into the West Indies the continental tropidurines became extinct north of Panama; or 2) that tropidurines and sceloporines diverged in South and North America, respectively, following some event which caused the separation of their common ancestral stock, e.g., the Eocene opening of the Panamanian portal, that *Leiocephalus* evolved in the West Indies from a South American tropidurine immigrant, and that the Florida fossils represent an invasion from the islands to the North American mainland.

Because of the close geographic proximity of Florida to the West Indies, and the inconclusive evidence (Estes and Tihen, 1964, p. 466) for the former existence of tropidurines elsewhere on the mainland north of Panamá, the latter alternative appears more reasonable. If this is correct, then *Leiocephalus* must have achieved its distinctiveness in the West Indies at least by mid-Cenozoic. The former existence of *Leiocephalus* on Jamaica and Barbuda clearly indicates that the genus must have occurred throughout most if not all of the West Indies in the past. Furthermore, the presence of extinct species of *Leiocephalus* in three of the four large West Indian lizard faunas that have been studied to date indicates that the current distribution of the genus may not reflect the extent of its range and structural diversity even in the very recent past.

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